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A Leptosporangiate Fern *Tempskya uemurae*, sp. nov. (Tempskyaceae) from the Upper Cretaceous (Santonian) of Iwate Pref., Japan

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A new species of the Cretaceous leptosporangiate fern family Tempskyaceae, *Tempskya uemurae* sp. nov. from Iwate Prefecture, Japan, is described based on a silicified false stem. The age of the fossil is estimated as Late Cretaceous (Santonian). The new species is characterized by small rhizomes, very short internodes, and mostly parenchymatous cortex and pith. This is the second species of the genus from Japan. The two *Tempskya* species from Japan represent the latest records of the extinct family Tempskyaceae, which were widely distributed in the mid-latitudes of the northern hemisphere during the Cretaceous.

Key words: anatomy, Cretaceous, fern, fossil, Japan, silicified, Taneichi Formation, *Tempskya uemurae*.

Tempskya Corda (1845) is a fossil genus of the leptosporangiate fern family Tempskyaceae, which are found exclusively from Cretaceous beds in the northern hemisphere. Species of this genus are reconstructed with a characteristic tree habit standing with a unique false stem consisting of numerous slender rhizomes less than 1.5 cm in diameter and a large number of intermingled adventitious roots enclosing the rhizomes (Andrews & Kern 1947).

More than 15 species have been reported from England, Ireland, northern France, Germany, Czechoslovakia, western Kazakhstan, Uzbekistan, Russian Far East, Japan, and the United States. Most of these species are restricted to the Lower Cretaceous or up to the lower Upper Cretaceous (Cenomanian), except *T. iwatensis* H. Nishida (1986) from the Santonian of Japan (Table 1). Ash & Read (1976) and Tidwell & Hebbert (1992) have made comprehensive studies of the taxonomy of *Tempskya*. Since the *Tempskya* species are clearly definable based on anatomical characters, recent taxonomic studies of the genus tend to exclude anatomically less-informative species, such as *T. pulchra* Corda (nominal type of the genus), *T. whitei* Berry (1911), *T. peregrina* Prynada (1945), *T. yattsenko-khmelevskii* Shilkina et Khudaiberdyev (1982), and *T. neumyvakinii* Popov (1996).

The new specimen described here was collected by Dr. Kazuhiko Uemura, National Science Museum, Tokyo, on the seashore of Oh-hama, Yagi, Taneichi, Kunohe-Gun, Iwate Prefecture, Japan during a field survey in 1984. The first species of *Tempskya* from Japan, *T.*

TABLE 1. Anatomically preserved *Tempskya* species comparable to the present fossil.

Species	Occurrence*	Age
T. rossica Kidston et Gwynne-Vaughan (1911)	Mugodzhar; Kazakhstan	Senonian?
T. knowltoni Seward (1924)	MT, UT; USA	Late Albian - Early Cenomanian
T. grandis Read et Brown (1936)	UT, WY; USA	Late Albian
T. minor Read et Brown (1936)	ID, NV, UT, WY; USA	Late Aptian - Albian
T. wesselii Arnold (1945)	MT, OR, UT; USA	Late Albian
T. wyomingensis Arnold (1945)	UT, WY; USA	Late Albian
T. superba Arnold (1958)	NV, UT; USA	Late Albian?
T. reesidei Ash et Read (1976)	NM; USA	Late Albian
T. zelleri Ash et Read (1976)	NM, UT; USA	Late Albian
T. iwatensis H. Nishida (1986)	Iwate, Japan	Santonian
T. jonesii Tidwell et Hebbert (1992)	UT, USA	Albian - Cenomanian
T. stichkae Tidwell et Hebbert (1992)	UT, USA	Albian
T. readii Tidwell et Hebbert (1992)	UT, USA	Late Early Cretaceous
T. uemurae H. Nishida (present study)	Iwate, Japan	Santonian

* ID, Idaho; MT, Montana; NM, New Mexico; NV, Nevada; OR, Oregon; UT, Utah; WY, Wyoming.

iwatensis, was found at the same locality. The locality and details of the geological setting and age determination are described in Nishida (1986). Alhough the present specimen was found isolated on a sandy shore, there is little doubt that it was washed out from upper part of the middle Okonai Member of the Taneichi Formation, which is dated as Santonian based on marine fauna (Terui *et al.* 1975; Matsumoto 1977). The underlying Uge Member of Campanian age contains rich palynoflora composed of 115 form-species of pteridophyte spores, 90 gymnosperm and 85 angiosperm pollen grains (Takahashi & Sugiyama 1990).

The anatomical terms in this description are the same as those used by Nishida (1986) based on general terminology for fern anatomy. For example, rhizome is used instead of stem, which is used for the individual rhizome of *Tempskya* false stem by some authors.

Material and Methods

The collected specimen was a whitish-gray silicified stem, about 20 cm long and oval in transverse section with short and long diameters of 9 and 17 cm, respectively. It was sectioned transversely at about one fourth of the way from one end using a slab saw with a diamond blade. Acetate peels were made using full-strength, commercial grade (46%) hydrofluoric acid (Joy *et al.* 1956; Basinger & Rothwell 1977). Peel specimens were mounted in Canada balsam, and examined using an optical microscope (Olympus BX 50). Fuji Neopan F film was used to obtain 35 mm b/w negatives. Digital images were obtained using a CCD TV camera (SONY DXC-9000) attached on an optical microscope (Leica DMR) and were processed into a plate using Adobe Photoshop 4.0.1J.

Results

Systematic Description

Order Filicales

Family Tempskyaceae Read et Brown, 1937

Genus *Tempskya* Corda, 1845

Tempskya uemurae H. Nishida, **sp. nov**. (Figs. 1-15)

Diagnosis. Fern false stem, 9-17 cm in diameter, radially symmetrical. Individual rhizome 2.5-3.0 cm in diameter, bifurcate and dorsiventral, departing 12 to 13 leaf bases in three alternate rows at 1 cm. Internodes very short, generally showing 4-5 leaf traces in one transverse section. Stele solenostelic with xylem plate containing abundant parenchyma. No clear histological zonation in cortex and pith, both parenchymatous except outer 3-5 layers of sclerotized cells of cortex.

Repository. Holotype NSM-PP9950 (original specimen and microscopic slides) in Paleobotanical Collections at Department of Geology and Paleontology of National Science Museum, Tokyo.

Locality. Oh-hama, Yagi, Taneichi, Kunohe-Gun, Iwate Prefecture; 40°21'N, 141°45'E.

Horizon and age. Taneichi Formation; Upper Cretaceous (Santonian).

Etymology. The specific name honors Dr. Kazuhiko Uemura who found the specimen.

Description. The round and smooth contours of the specimen suggest that it was considerably worn in the sea after it was washed out of the original sediments (Fig. 1). The transverse oval form was probably caused by lateral compression during diagenesis, because most of the delicate tissues such as the rhizome pith parenchyma are squashed perpendicularly to the longer axis of the stem cross section.

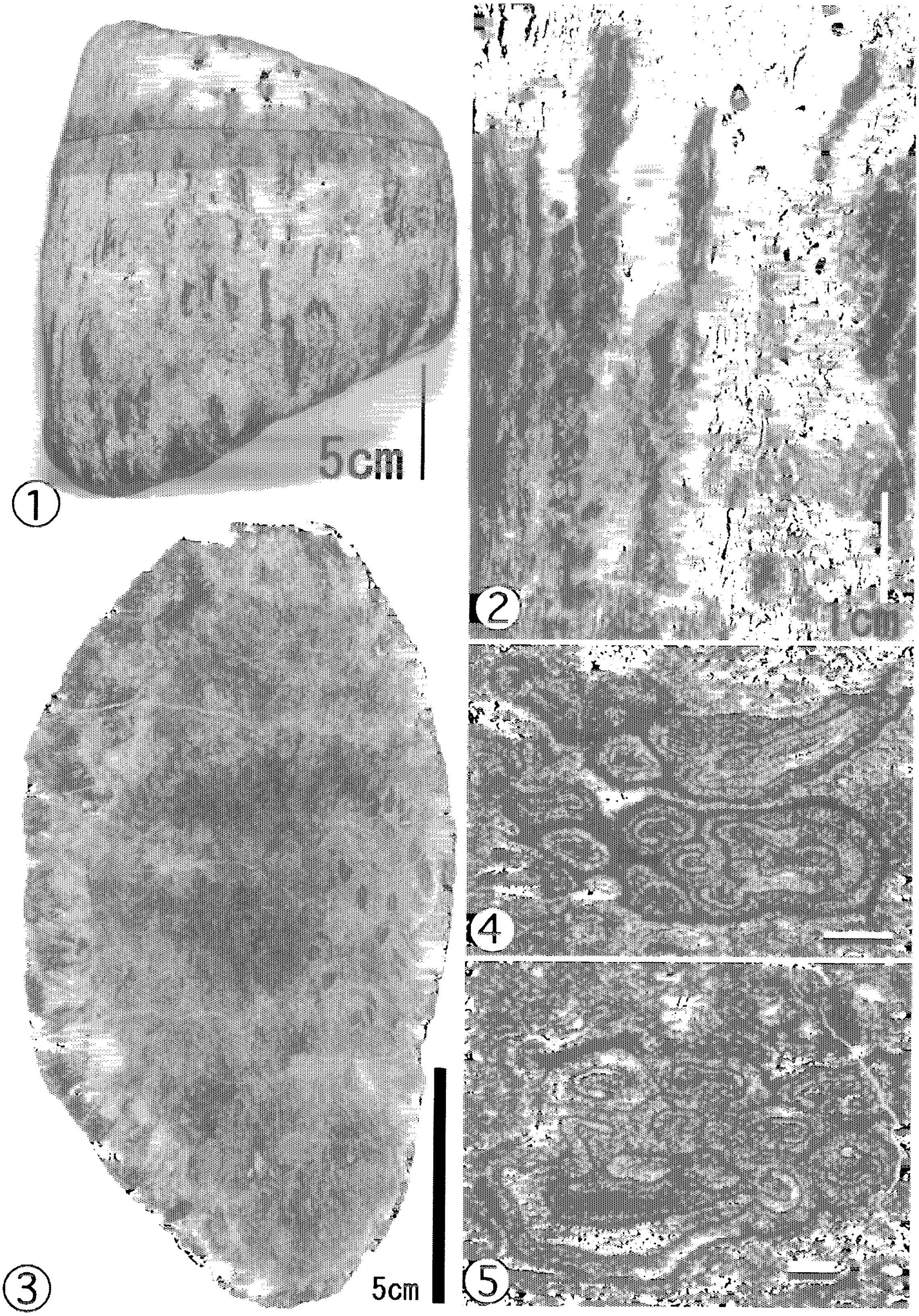
More than 50 rhizomes are exposed on the external surface as black longitudinal striations of varying length. The longest exceeds 7 cm and some are bifurcating. All exposed rhizomes show their dorsal side towards the outside of the stem, bearing leaves in three rows. Therefore, three alternate rows of petiole bases are seen on the dorsal surface of some rhizomes (Fig. 2). There are 12 to 13 leaf bases in 1 cm. The growth direction (top of the false stem) was identified from the bifurcation pattern of each rhizome and the leaf trace dorsiventrality seen in the petiole base section.

In one transverse section, there are about 270 rhizomes embedded in a dense mat of adventitious roots that constitute the major part of the false stem characterizing *Tempskya* (Fig. 3). Near the stem periphery, some free petioles are preserved. In the false stem, the rhizomes give rise to leaves toward the nearest stem periphery. Therefore, the false stem is radially symmetrical. The rhizomes and roots are well-preserved, although most tissues show some signs of fungal decay. The descriptive terms of taxonomically important characters are in conformity with those used by Nishida (1986).

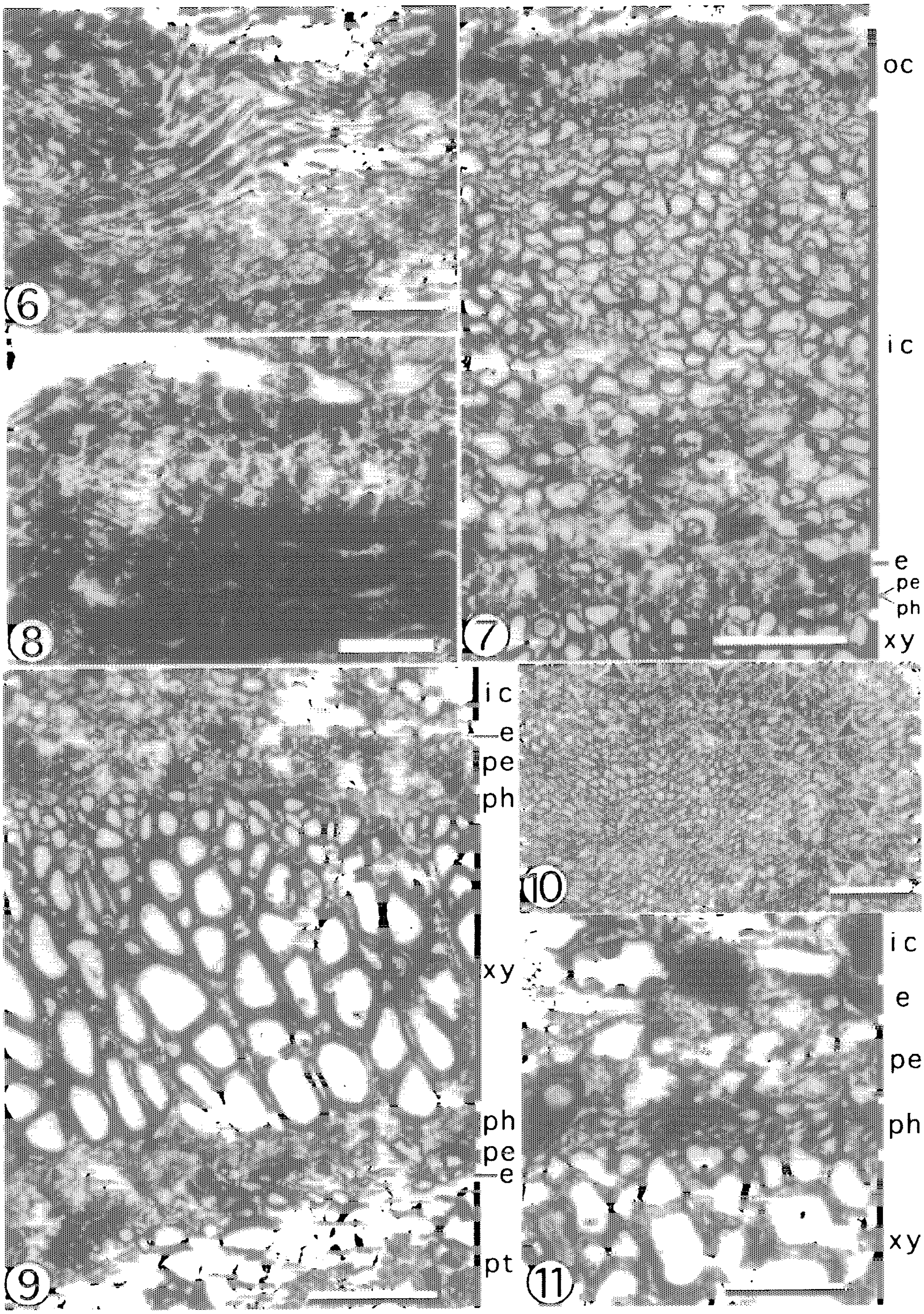
The rhizomes are slender, 2.0-4.0 mm in diameter, solenostelic, with very short internodes (Figs. 3-5). In cross section, there are generally four to five overlapping leaf bases. Bifurcation of the rhizome occurs giving rise to leaves, so that more than seven leaf bases overlap in sections of dividing rhizomes. The roots arise endogenously either from the periphery of the stele, or the abaxial side of the petiole trace.

The epidermis is not clearly definable due to a dense mat of dermal hairs (Fig. 6). The hairs are about 7.5 μm thick at base, more than 0.3 mm long, and contain dark substance. At lower magnification, the cortex appears to have three zones: thin outer, brownish middle, and thickest inner (Fig. 5). However, careful examination at high magnification shows that the middle zone consists of parenchyma cells degenerated and squashed by fungal activity. In better-preserved cortex, there is no histological difference between the middle and inner zones (Fig. 7), and the cortex is two-layered. The outer cortex is 3-5 cells thick, composed of sclerenchyma cells, 5-15 μm across, containing dark substance (Fig. 8). The inner cortex is 17-20 cells thick, consisting of large parenchyma cells, 10-37 μm across. The cells are larger near the periphery of the stele.

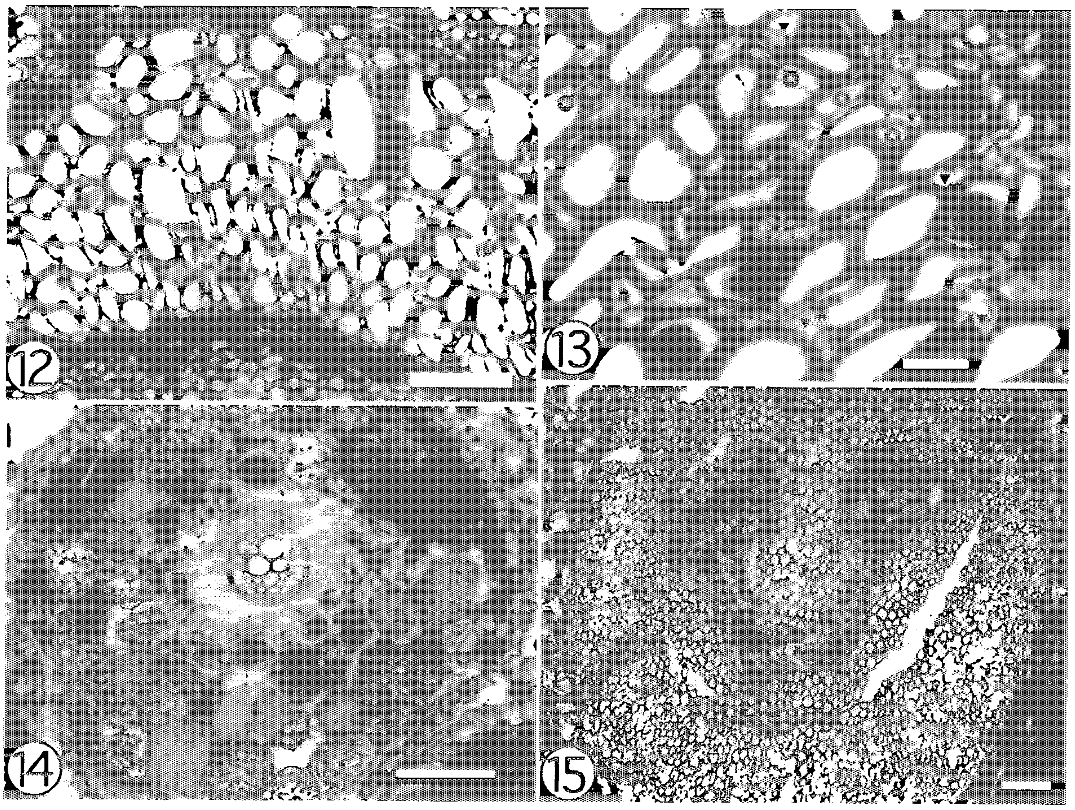
The solenostele consists of amphiphloic



FIGS. 1-5. *Tempskya uemurae*, sp. nov. Fig. 1. Lateral view of original false stem sectioned transversely into two parts at a horizontal line. Fig. 2. Close-up of surface rhizomes, showing dichotomy. Note dorsal leaf bases arising in three alternate rows. Fig. 3. Cross section (cs) of false stem. Slide Btop#5. Figs. 4, 5. Cs of rhizomes. Dorsal side of rhizome to left in Fig. 4, above in Fig. 5. Note leaf traces arising in three alternate rows. Dark tissues in cortex and pith are squashed parenchyma. Btop#2b. Scales = 1 mm.



FIGS. 6-11. *Tempskya uemurae*, sp. nov. Fig. 6. Dermal hairs on rhizome surface. Cells of outer cortex are degraded. Btop#2b. Scale = 0.1 mm. Fig. 7. Cs of cortex. Note parenchymatous inner cortex (ic). Outer cortex (oc) is mostly degraded. e, endodermis; pe, pericycle; ph, phloem; xy, xylem. Abot#1a. Scale = 0.1 mm. Fig. 8. Fibrous sclerenchyma of outer cortex. Dermal hairs are lost. Dark tissues below are degenerated parenchyma of inner cortex. Abot#1a. Scale = 50 µm. Fig. 9. Cs of rhizome vascular bundle. pt, pith. Abot#1a. Scale = 0.1 mm. Fig. 10. Cs of pith consisting of parenchymatous cells. Arrowheads indicate alignment of inner endodermis. Btop#2b. Scale = 0.2 mm. Fig. 11. External periphery of rhizome vascular bundle. Btop#2b. Scale = 50 *µ*m.



FIGS. 12-15. *Tempskya uemurae*, sp. nov. Fig. 12. Cs of rhizome xylem, showing scalariform thickenings. Note intercellular spaces between tracheary walls. Btop#2b. Scale = 0.1 mm. Fig. 13. Xylem enlarged. Note thick secondary walls of small tracheary tips marked with stars and thin walls of xylem parenchyma marked with reversed triangles. Abot#1a. Scale = 50 µm. Fig. 14. Cs of root. Larger cells of outer cortex infected by fungi. Inner cortex and endodermis subsequently surround central vascular bundle. Abot#1b. Scale = 0.1 mm. Fig. 15. Cs of free petiole. Btop#2b. Scale = 0.2 mm.

collateral vascular bundles and a well-developed pith (Fig. 9). The pith parenchyma cells are large and 11-36 µm in diameter (Fig. 10). The central portion of pith in most rhizomes is brownish and squashed, also due to fungal invasion. The vascular bundle is enclosed by poorly preserved endodermis (Figs. 9, 11). There is a pericycle 1-2 cells wide inside the endodermis. The phloem is composed of an external alignment of small protophloem cells, and internal metaphloem, 2-3 cells thick. The xylem plate undulates more or less according to departure of leaf traces. The protoxylem position is not clearly identifiable. Xylem maturation is probably mesarch. Metaxylem tracheids have scalariform thickenings (Fig. 12). Small parenchyma cells are dispersed in the xylem plate, sometimes forming masses of several cells (Fig. 13). Some authors doubt the presence of xylem parenchyma in Tempskya, claiming that the smaller cells that appear to be parenchyma in the xylem are the tips of overlapping tracheids (Tidwell & Hebbert 1992). However, in this specimen, the parenchyma and tracheary tips are clearly defined based on the wall thickness (Fig. 13). The xylem parenchyma cells lack secondary thickenings and are short when sectioned obliquely to longitudinally.

In mature roots, the xylem is diarch (Fig. 14). The roots are similar to the roots of other species of *Tempskya* in general structure. The cortex is two-layered. The outer cortex consists

TABLE 2. Anatomical comparisons of *Tempskya* species.

Species	False stem		Size of rhizome (mm)	Internode length**	Cortex***			Pith***		Xylem paren-chyma
	Diameter (cm)	Symme-try*			Outer	Middle	Inner	Outer	Inner	
T. rossica	5.5 - 9.5	R	6.0 - 7.0	medium	pa	sc	pa	pa	sc	2
T. knowltoni	1.5 - 6.5	D	2.5 - 3.5	medium	pa	sc	pa	pa	sc	1-2
T. grandis	10.4 - 12.2	R	4.6 - 6.0	short	pa	sc	pa + sc†	pa + sc†	sc	3
T. minor	9.0 - 14.4	D-R	2.0 - 3.5	medium	pa	sc	pa	pa	sc	1
T. wesselii	7 - >40	R	4.0 - 5.0	long	pa	sc	pa + sc†	pa	sc	3
T. wyomingensis	?	R	6.0 - 8.0	medium	pa	sc	pa + sc†	pa	sc	3
T. superba	>12	R	10.0 - 15.0	short	pa	sc	pa + sc†	pa + sc†	sc	3
T. reesidei	10 - 30	R	3.0 - 5.0	medium	pa	pa islands in sc		sc	pa	2
T. zelleri	17	R	3.0 - 8.0	long	pa	sc	pa	pa	sc	2
T. iwatensis	7 - 12	R	2.7 - 3.6	medium	sc	pa		tw	sc	3
T. jonesii	30	R	4.0 - 4.5	long	pa	sc	pa	pa	sc	1
T. stichkae	17	R	6.0 - 8.0	medium	tw	sc	pa††	pa††	sc	1
T. readii	?	R	5.0 - 7.0	medium	tw?	sc	sc	sc		1
T. uemurae sp. nov.	9 - 17	R	2.0 - 4.0	short	sc	pa		pa		3

* R, radially symmetrical; D, dorsiventral.

** long, 1 leaf trace in one cross section; medium, 1 - 3 traces; short, >3 traces.

*** pa, parenchyma; sc, sclerenchyma (fibrous); tw, thick-walled cells.

† Irregular nests of sclerenchyma.

†† Three zones of irregular sclerenchyma present (Tidwell and Hebbert 1992).

of larger cells, while the inner cortex is of smaller thin-walled cells. Root hairs are sometimes found. More than one species of fungi at various life-cycle stages occur in the roots. The fungi are most abundant in the outer cortex. Some exhibit features of V-A mycorrhizal fungi similar to those reported in the root of *T. wyomingensis* (Tidwell & Hebbert 1992).

Petioles are slender, 1.8 x 1.9 mm in diameter, and do not persist long in the tissue of the false stem (Fig. 15). Free petioles are most frequently found near the stem periphery, although the tissues are black in contrast to the brown color of rhizomes and roots, suggesting faster degeneration. Petioles are hairy only near the base. The petiole vascular bundle is similar in shape to the bundles of other *Tempskya* species. In the free petiole, the fundamental tissue consists of parenchyma, excepting the adaxial periphery of the cortex, where cells are slightly sclerotized.

Discussion

If the original uncompressed trunk was circular in cross section, the diameter is estimated to have been about 12 cm. The false trunk is radially symmetrical in the arrangement of rhizomes like most *Tempskya* species, indicating that the plant had a small tree habit with leaves propagating in all directions.

At present, there are 13 *Tempskya* species deserving anatomical comparison with this new specimen (Tables 1, 2). *Tempskya* species are defined on the basis of combinations of selected characters. Although evaluation of taxonomically valuable characters differs slightly according to the author (Read & Brown 1937; Andrews & Kern 1947; Ash & Read 1976; Nishida 1986; Tidwell & Hebbert 1992), species are clearly defined without significant conflict. The new species, *T. uemurae*, is characterized by slender rhizomes, very short internodes, three rows of leaf traces, mostly parenchymatous cortex, and parenchymatous pith (Table 2).

The amount of xylem parenchyma has been used as one comparable character. However, Tidwell & Hebbert (1992) suggested the possibility that the slender tips of tracheids have been misidentified as parenchyma. Since *T. uemurae* has clearly definable xylem parenchyma, I included this character for species comparison.

Except for the two species from Japan, *Tempskya* species are found in the Lower Cretaceous strata with some extending to the lower Upper Cretaceous (Cenomanian) (Table 1). The Santonian age of *T. iwatensis* and *T. uemurae* is the latest record of the genus. The Upper Cretaceous strata from northern Japan include taxa typical of Lower Cretaceous or much older flora, such as *Cycadeoidea* (Nishida 1991, 1994). At present, there is no persuasive explanation for the presence of these older elements in the Late Cretaceous flora of Japan. *Tempskya uemurae* shows that the tempskyas were still a rich part of the flora at the edge of east Asia during the Late Cretaceous.

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